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THE BOTANICAL REVIEW

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PHYSIOLOGIC SPECIALIZATION AND GENETICS OF THE SMUT FUNGI. II[1]

C. S. HOLTON[2]

INTRODUCTION

Much has been added to the store of information on physiologic specialization and genetics of the smut fungi in the 12-year period since Christensen and Rodenhiser (14) reviewed the literature on this subject. These authors referred to the complicating implications of physiologic specialization and genetics in the fungi in relation to plant disease control. Experiences of the last decade should have erased any doubt of the practical significance of this problem. During this time devastating epiphytotics of black stem rust occurred which were traceable to races of the rust fungus that originated by hybridization on the common barberry, its alternate host. Also during this period the Victoria blight and smut races specialized to Victoria oats came into prominence, forcing abandonment of commercial production of varieties with Victoria germ plasm. New races of wheat bunt appeared on varieties that had been resistant, and the distribution of known races was extended into new regions. These examples indicate the dynamic nature of plant disease agents and serve to reemphasize the practical problems of plant disease control resulting from pathogenic specialization in the fungi. Consequently, an extension of Christensen and Rodenhiser's (14) review of specialization and genetics in the smut fungi seems appropriate at this time.

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PHYSIOLOGIC SPECIALIZATION

As used here and in the previous review, the term "physiologic specialization" refers to the occurrence of entities within morphologic species that differ from each other in one or more physiologic characters. Economically the most important of these characters is pathogenicity. Hence most of the recent workers on specialization in the smuts have concentrated on pathogenic specialization. This is especially true with the cereal smuts, though some attention has been given to this problem in other smuts. Race differentiating characters other than pathogenicity include culture characters, host morphology, minor differences in spore morphology and differences in spore germination. This review will treat the subject in the broad concept, considering specialization of all kinds in individual smut diseases. For the sake of convenience the term "smut" will be used synonymously with the species name, and, for the most part, the nomenclature of Stevenson and Johnson (100) is accepted as standard.

WHEAT SMUTS. The full implication of specialization in the smuts is perhaps best exemplified by bunt or stinking smut (*Tilletia caries* (DC.) Tul. and *T. foetida* (Wallr.) Liro) of wheat. The world-wide economic importance of this smut is reflected in the contributions by workers from many countries. This is especially true in the United States where continuing specialization studies were reported intermittently by Rodenhiser and Holton (52, 92) for more than 20 years. Since the first review they have added 12 pathogenically distinct races to the 19 previously reported, bringing the total number described by them to 31. Twenty-nine of these were found in the United States and the other two were from Mexico. The races occurring in the United States were distributed throughout the major wheat regions, the greatest concentration being found in the Pacific Northwest. The relationship of the problem of pathogenic specialization to the practical problem of breeding smut-resistant wheat varieties was emphasized by the tabulation of the reactions of a large number of wheat varieties to 26 of the races (92). The importance of varietal testing under different environmental conditions was emphasized by the fact that certain varieties did not react the same when grown in different localities (91).

Other work on specialization in wheat smut has demonstrated the presence of at least ten races in each of Rumania (93) and

China (131, 132), probably seven in Argentina (10) and an undetermined number in Russia (97).

As pointed out previously, distinguishing characteristics other than pathogenicity have been observed in the bunt fungi. For example, races may differ in size and color of spores, size and shape of bunt balls (sori), prominence of spore wall reticulations, relative degree of stunting the host, rate and kind of spore germination, and nuclear behavior (52, 97). Lowther (68) classified 26 races into several groups on the basis of germination rate. Temperature was an important factor in rate of germination, and, in the dwarf bunt race of *Tilletia caries*, germination occurred best at 5° C. (67). This race usually can be identified by characters other than pathogenicity (43, 47, 48, 114, 116, 121, 122).

Evidence continues to accumulate that host selectivity is an important factor in the establishment of new races. This selective influence may be in the direction of either greater or less pathogenicity. For example, Vielwerth (120) concluded that the pathogenicity of bunt populations gradually decreases when they are constantly propagated on moderately susceptible wheat varieties and that such varieties play an important selective part in the development of physiologic races of bunt. In studies with experimental hybrids Holton (45) found that the highly susceptible variety Hybrid 128 tended to promote the establishment of weakly pathogenic races with a narrow host range, while resistant varieties promoted the establishment of races with high virulence and a wide host range. This is substantiated by practical experience. Races of high virulence and wide host range are most populous in regions where new smut-resistant varieties are frequently introduced (92).

Specialization in *Ustilago tritici* (Pers.) Rostr. was demonstrated by Rodenhiser (89) in 1926 when he described three races of this species based on culture characteristics among haploid lines from one pathogenic type. Lange de la Camp (62) made similar observations. Piekenbrock (83) observed a differential reaction of one wheat variety to two collections of loose smut and thereby established in 1927 that pathogenic specialization exists in this species. His work was extended by Grevel (27) who identified four races in 48 collections of loose smut, three of which were from Germany and one from Turkey. In the meantime Tapke (101) had obtained evidence of pathogenic specialization in this species in the United States, and Radulescu (85) reported several races in

Germany. Since then systematic studies of this problem have been made by several workers.

Hanna and Popp (32) identified two races of *Ustilago tritici* in Canada, and later Hanna (30) found two additional races, one of which apparently originated as a mixture in one of the two original races. In the United States Moore (73, 74) was able to identify five races of loose smut by the differential reaction of certain bread and durum wheats. Most of the collections tested were able to infect one or the other group but not both. A few collections, however, attacked certain varieties of both groups. Caldwell and Compton (7) reported a high degree of specialization among seven collections of loose smut on seven varieties of soft red winter wheats.

Oort (77, 78) reported that specialized races of loose smut from winter wheat would not attack spring wheats, nor would those from spring wheat attack winter wheats. Later (79) he described six races of this smut based on the reaction of nine varieties of spring wheat to ten collections originating in several countries. In China, Wang (124) identified two races of loose smut and observed that the race from *Triticum turgidum* would not infect common wheats, and the one from the latter failed to infect *T. turgidum,* an observation which was confirmed by Yin (127). Pal and Mundkur (80) reported the occurrence of two races in India.

Bever (2) suggested a standard basis for race identification in wheat loose smut. He described 11 pathogenic races in 52 collections of loose smut from 15 states of the eastern soft wheat region. Ten varieties were used as differential hosts, and the races were separated by the resistance or susceptibility of these varieties. Race 1 was the most widely distributed, being found in seven of the 15 states and represented by 11 collections. Races 4, 8 and 9 were collected only once each.

Though not extensively investigated, specialization in flag smut (*Urocystis tritici* Koern.) has been reported from several countries of the world. Verwoerd (119) found no evidence of specialization among collections tested in South Africa, while Yu et al. (130) identified 12 races in China. These races were distinguishable by the reaction of four common and one poulard variety of wheat. Two races of flag smut, designated as 1 and 2, are known in the United States (50), the former occurring in the Midwest and the latter in the Pacific Northwest. In Pakistan, Hafiz (28) tested 11

collections of flag smut from six countries and identified four distinct pathogenic entities. His races 1 and 2 were the same as 1 and 2 from the United States, the latter being represented by collections from Italy and Australia as well. Race 3 was represented by three collections from China and one from Cyprus, while race 4 was represented by two collections from Pakistan.

Specialized races of *Urocystis tritici* on culture media were reported by Wu (126) who investigated three cultures on 12 different media. Though growth rate was relatively slow, the three races were distinctly different on five of the media.

OAT SMUTS. In 1940 Reed (86) described and numbered 29 races of *Ustilago avenae* (Pers.) Rostr. and 14 of *U. kolleri* Wille. This was a culmination of a long series of reports on specialization in the oat smuts by him and his co-workers. About half of these were from the United States, the remainder from foreign sources. Later Reed et al. (87, 88) described two additional races of *U. avenae,* both of which were able to infect Victoria, formerly resistant to all known races. Hansing et al. (33, 34) found two additional Victoria-type races. Tervet (109) identified three races of each species out of 79 collections tested and called attention to certain problems encountered in race studies. Inconsistency in the reaction of tester varieties to certain races in different years was noted (110), and later it was shown that this could result from using seed lots of the same variety from different sources. Quality of seed also was found to be an important factor in varietal reaction (111).

Holton and Rodenhiser (53) emphasized the need for correlating studies on physiologic specialization in the oat smuts with the development of smut-resistant varieties of oats and proposed the adoption of a standard system of race identification in these smuts. Twenty-two races were identified among 218 collections from all sections of the United States, and provision was made for using these races to test for resistance in oat varieties and lines used in breeding new varieties.

BARLEY SMUTS. Physiologic specialization in the barley smuts involves three species—*Ustilago nuda* (Jens.) Rostr., *Ustilago nigra* Tapke, and *U. hordei* (Pers.) Lagerh. Tisdale and Griffiths (115) recognized two pathogenic races of *U. nuda.* This was prior to the recognition of *U. nigra* which possibly could have been the species with which they were working. Moore (73) obtained in-

consistent results and was unable to identify races of *Ustilago nuda*. Oort (77) and Thren (113), however, were able to demonstrate that collections of this species from winter barley would not infect spring barley, while those from spring barley would not parasitize winter barley. In the black or seedling-infecting loose smut (*Ustilago nigra*) Josephson (56) identified eight races from 100 collections, based on the reaction of nine varieties. In 1943 Tapke (105) found seven races of this species in 168 collections from 23 states. Race 4 was most prevalent, occurring more often than all other races combined. Two additional races were reported in 1951 (108), along with four races identified in 16 collections from Israel. Three of the races from Israel were pathogenic on Pannier which has been immune from the nine races known to occur in the United States.

Pathogenic specialization in *Ustilago hordei* (Pers.) Lagerh., first demonstrated by Faris and later confirmed by Allison and Tapke, has been further investigated in more recent years (14). Tapke (107) identified five races in addition to eight previously reported (102), making the total 13. These were found among 444 collections of smut from 33 states. Race 6 was the most widespread, representing 61 per cent of all the collections. Semeniuk (96) identified four races in 12 collections of *U. hordei* in Canada, and Pugsley and Vines (84) were able to recognize three races in Australia. Yu (128) found five races in 280 collections of covered smut in Kiangsu Province, China. These races were differentiated by the reaction of three barley varieties. Later Yu and Fang (129) identified nine races of *U. hordei* in 84 collections from southwestern China.

MISCELLANEOUS SMUTS. Specialization studies in some of the grass smuts have gained impetus in recent years. Fischer (17) described a race of *Ustilago striaeformis* (Westd.) Niessl. that differed from previously recognized races by the fact that the spores did not require an after-ripening period for germination. Kreitlow (60) recognized two biotypes of *Ustilago striaeformis* f. *agrostidis* on agar, and later (61) he observed that colonies of this species fell into two distinct types, one flat and lustrous, the other fluffy and raised, the color of both being pale buff. Two biotypes were differentiated on the basis of rate of growth. Leach et al. (64, 65) also reported two types of colonies in this species. One was typically

mycelial and the other broke up into sporidia-like fragments. Thirumalachar and Dickson (112) obtained several biotypes of *U. striaeformis* in culture, including both sporidial and mycelial types. Fourteen differential grass species were used by Fischer (18) to establish the identity of eight physiologic races of *Ustilago bullata* Berk., and Meiners (72) reported differences in culture characteristics of these same races. Wang (123) identified six physiologic races of *Ustilago crameri* Koern. by the reaction of 11 millet varieties. Varying numbers of cultural biotypes in several species were reported by Martin and Kernkamp (70), and Hirschhorn (38, 39) recognized about 500 cultural lines of *Ustilago zeae* in seven populations from as many geographic localities. Similar observations on *Sphacelotheca sorghi* were made by Vaheeduddin (118) who reported 16 different cultural biotypes among 74 haploid lines from 28 chlamydospores.

GENETICS

Most permanently distinctive characters in the smut fungi are controlled by genetic factors, and the heritability of certain characters is well established. In their review Christensen and Rodenhiser (14) discussed the mechanism of heredity and the nature of sex compatibility factors, chlamydospore and culture characteristics, and pathogenicity. Research findings since then have contributed to broadened concepts of genetic relationships in several of the smuts. Among these *Ustilago zeae* has been studied the most intensively. Investigations with this species have covered a wide range of genetic phenomena, thus making it an appropriate basis for discussing this subject.

COMPATIBILITY FACTORS. Sex compatibility is basic to genetic studies in the smuts. Consequently determination of compatibility factors is preliminary to a genetic study of other characters. As shown in the previous review (14), sex ratios vary widely in different species and races, and further evidence has accumulated that indicates regularity and irregularity in sex ratios of certain species. For example, Stakman et al. (99) obtained evidence pointing to gradations in degree of maleness and femaleness in certain lines of *Ustilago zeae* (Beckm.) Ung., and a similar situation was described for *Ustilago avenae* and *U. perennans* Rostr. by Holton and Fischer (49). Simple 2:2 sex factor ratios have been established for *Usti-*

lago bullata (19) and *Ustilago lorentziana* Thüm. (31). Though multiple sex factors were reported earlier, Holton (46) obtained evidence for only two sex factors in *Tilletia caries* and *T. foetida*, as indicated by the infective capacity of paired monosporidial lines.

Multiple sex factors were found in *Sphacelotheca sorghi* (Link.) Clinton by Vaheeduddin (118) who demonstrated up to 60 sexual groups by mating 74 monosporidial lines in all possible combinations. Fischer (20) observed six sex groups in cultures of *Ustilago striaeformis* f. *hordei* taken from 12 collections, whereas earlier tests with cultures from one collection had indicated only two sex groups.

In a general survey of heterothallism in the smuts Whitehouse (125) questions the evidence for multiple sex factors and states that all claims for the existence of complex types of heterothallism are based on faulty reasoning. He discusses each reported case of multiple sex factors and concludes, from theoretical considerations, that heterothallism in all species of smuts thus far investigated is controlled by a single pair of allelomorphs. Since Whitehouse (125) presented no data, the validity of his conclusion is questionable.

LYSIS. Kernkamp and Petty (59) observed 25 types of germination in chlamydospores of field collections, crosses and diploid monosporidial lines of *Ustilago zeae*. Considerable variation in type for each collection was found, but there was a tendency for a given type to predominate. The type in which the promycelia form hyphal branches instead of sporidia was predominant in five collections. Next in line was the type in which the spore functions as the basal cell of the promycelium, thus producing sporidia directly from the spore. This type predominated in four collections. Two opposite promycelia on each spore, promycelia with four cells, and lysing promycelia also were among the five most prevalent types. Erratic germination resembling lysis in spores from a cross between *Ustilago striaeformis* and *U. bullata* was reported by Fischer (22).

Lysis has been observed in several smut species (13, 19, 46, 63). It may occur in the promycelium (13, 63) or in the sporidia (19, 46). Its heritable nature in *Sphacelotheca sorghi* was demonstrated by Laskaris (63) who stated that degree of abnormality in spore germination appeared to be correlated with degree of lysis. In certain crosses involving the lysis character the spores, promycelia and

sporidia were larger than those of normal crosses (63). Heritability of the lysis character in *Ustilago zeae* was reported by Chilton (13) who found that only certain lines carried the lysis factor or factors and that their operation was restricted to the period of meiosis. Chlamydospores of hybrid origin involving lysis factor lines had a tendency to produce exceptionally large numbers of solopathogenic lines. On the other hand, lysis tendency was not associated with solopathogenicity in *Sphacelotheca sorghi* (63). Solopathogenic lines were encountered infrequently by Schmitt (95) who found only three in 4,000 monosporidial lines of *U. zeae.*

Lysis in the sporidia of *Ustilago bullata,* as reported by Fischer (19), was operative against saprophytism but not against parasitism. Half of the sporidia from a promycelium developed into colonies, while the other half budded several times and then underwent complete lysis. In four out of five collections the lysis factor was sex-linked. This was shown in their reactions to each other and to lines representing other collections and species. Expression of lysis in the sporidia of *Tilletia foetida,* race L-8, was similar to that in *U. bullata.* Half of the isolated sporidia of L-8 developed colonies, while the other half initiated growth and then underwent lysis (46). It was invariably associated with one sex group and was designated as a sex-linked lethal deficiency.

DELAYED REDUCTION. In connection with studies of lysis in *Ustilago zeae,* Chilton (12) obtained evidence of delayed reduction of the diploid nucleus in the promycelium. Monosporidial lines were obtained from 158 chlamydospores produced by crosses involving the lysis factor or factors. Both haploid and diploid sporidia were produced on the promycelia of three of these chlamydospores in such a way as to indicate that the first meiotic division was postponed to the second division of the diploid nucleus in one spore and to at least the third division in the other two. Schmitt (95) found that segregation of factors for color, for sex and for type of growth occurred in both the first and second divisions of meiosis.

MUTATION AND ADAPTATION. Gattani (25) obtained several diploid lines from a cross between a stable and a mutable haploid line. Of these, seven differed from each other and the parent lines in at least five characters, including pathogenicity. One of the diploid lines was mutable like the mutable parent. Numerous mutations

in this line were induced by growing it on media containing lithium, arsenic or uranium. Schmitt (95) likewise observed that the culture medium exerts an effect upon mutation rate. Fewer mutations occurred in cultures on corn-meal agar than in the same lines growing on more nutritive media.

Factors other than kind of culture medium may exert an effect on mutability in corn smut. Schmitt (95) found that temperatures above 20° C increased the frequency of mutations, whereas few mutations occurred below 20° C. Inbreeding for ten generations, ultra-violet radiation, X-rays and exposure of sporidia to temperatures near the thermal death point did not affect the frequency of mutation. The mutation rate of sporidial lines was about three times that of mycelial lines. In a study of physical and chemical adaptation and environmental "carry-over" in *Ustilago zeae*, Petty (82) found that cultures could be adapted to grow more readily on media of high arsenic concentration on which unadapted cultures failed to grow. At 32° C and 35° C one haploid line gave rise to 13 mutants, one temporary variant that persisted for two cultural generations, and two variants that did not persist beyond the generation of their origin. Mutations occurred frequently on arsenic media.

Perkins (81) emphasized the value of biochemical mutants in genetic studies and pointed out that their potentialities in the smuts have scarcely begun to be realized. He obtained and characterized stable biochemical mutants of *Ustilago zeae* and described 15 isolates with specific nutrient requirements. Segregation and recombination of mutant factors was obtained from crosses involving two and three loci at a time. Moulton (75) was able to extract auxin from *U. zeae* tumors and observed that pathogenicity of different strains was correlated with their ability to produce auxin in a synthetic medium. Feldman (15, 16) was able to correlate the physiological activities of lines and combinations of lines of *U. zeae* with pathogenicity rating, but there was no difference among these lines in the physiology of the galls. Cercos and Favret (11) found corn smut to be a powerful source of mitogenic radiation, and Haskins (36) reported the production of antibiotic substances designated as ustizeain.

Specifically sporidial and mycelial lines of *Ustilago zeae* are unalterably fixed, according to Kernkamp (57), while those of

intermediate tendency can be shifted either way by different environments. Addition of dextrose to the culture medium stimulated sporidial formation, while reduced nutrients and oxygen or additions of certain poisons and dyes to the medium promoted mycelial growth. Further evidence that genetic factors exert an influence on culture characters was shown by the fact that crosses between intermediate lines that were mostly sporidial gave rise to progenies that were mostly sporidial, while crosses between intermediate lines that were mostly mycelial increased the prevalence of mycelial lines in the progenies. Crosses between strictly sporidial lines failed to produce infection, although they were able to infect the host when crossed with mycelial lines. Thus it was concluded that strictly sporidial growth is limited by genetic factors and can not be changed by environment.

Though sporidial fusion in *Usilago zeae* rarely occurs, Bowman (5, 6) found this process to be markedly influenced by the nutritive value of the medium and by temperature. Fused sporidia occurred in distilled water and in one per cent malt-extract solution at the end of 15 to 20 hours at 20–24° C. According to Hirschhorn and Munnecke (40), the combining ability of lines may be altered by growing them on medium containing sodium arsenite. They reported that two lines of opposite sex lost their ability to combine following adaptation to an arsenic-containing medium and regained this ability after three transfers to an arsenic-free medium.

Munnecke (76) observed an unusual host response to certain paired monosporidial lines of *U. zeae*. Three pairs of white cultures produced leaf curling and distortions resembling smut galls which contained smut mycelium, but chlamydospores were not formed. Kernkamp and Martin (58) compared the virulence of pairs and composites of monosporidial lines of *U. zeae,* and found that the virulence of the composite inoculum approached that of the single pairs. In tests with two series of composites the reaction of the composite of both series was intermediate between the reactions of the two series. There was no evidence of antibiosis between lines in culture.

In an extensive study of the genetic basis for certain cultural and mutant characters in *Ustilago zeae,* Stakman et al. (98) crossed two haploid lines possessing several contrasting characters and obtained four monosporidial lines from a single chlamydospore of this

cross. Heritability was clearly demonstrated and segregation was on a 2:2 basis for sex, color, growth type, topography and mutability. It was concluded that *U. zeae* comprises an indefinite number of biotypes exhibiting slight or wide differences in all observable characters. Furthermore, new biotypes are continually being produced, both by mutation and by recombination of factors from inter-biotypic hybridization. It was noted, however, that the chlamydospore characters are remarkably uniform in all biotypes or combinations thereof.

Vaheeduddin (118) has shown that there are many haploid biotypes of *Sphacelotheca sorghi* and *Sorosporium reilianum* (Kühn) McAlp. which hybridize readily, and some of them mutate. Segregation and recombination of factors for sex, peridial color and pathogenicity occurred in hybrids between biotypes of *S. sorghi*. The behavior of intergeneric hybrids (*S. sorghi* × *S. reilianum*) indicated that such characters as type of sorus, chlamydospore morphology, culture characteristics and pathogenicity were transmitted in normal genetic fashion. Heterosis was suggested by the fact that the promycelia of intergeneric hybrid spores were much longer than those of the parent spores.

Martin (69) reported that characteristics of hybrids between *Sorosporium syntherismae* (Pk.) Farl. and *Sphacelotheca panicimiliacei* (Pers.) Bubak were intermediate between those of the parents. Spore size and spore markings were inherited independently in hybrids between these species. The factor for verrucose-spore walls behaved as a simple dominant over that for smooth spore walls. The implication of genetic factors in these species is indicated by the occurrence in *S. syntherismae* of a mutant line with buff sori (55). Cultures of the buff type were mycelial and stable, while those of the original type were sporidial with a pronounced mutant tendency. It was concluded that the buff smut arose by mutation and that the change possibly involved several factors.

HYBRIDIZATION. The potentialities of hybridization and mutation as sources of new races in the smuts are emphasized by the work with oats and barley smuts. From one inter-species hybrid Utter (117) obtained 13 races of covered smut and nine races of loose smut, including the parent races. The pathogenicity of some of the loose smut races was like the covered smut parent, and some of the covered smut races showed a pathogenicity like that of the

loose smut parent. Thus the factors for pathogenicity and gross morphology of the diseased plant were inherited independently. Leitzke (66) regards the appearance of new pathogenic types in spore mixtures used by him as the product of hybridization, reflecting the variable mode of inheritance of pathogenicity. From additional studies on a mutant buff smut of oats described earlier, Holton (41) concluded that pathogenicity of any race of *Ustilago avenae* or *U. kolleri* could be transferred to the buff race by hybridization. Segregation and recombination of factors for sex, pathogenicity and spore color were independent, thus making it possible to select for any one of several possible types in the segregating generation. Two types of sori produced by two races of *Ustilago avenae* were found to be controlled by different genetic factors (41). The factor for powdery sorus was dominant over that for indurate sorus, segregation and recombination being on a simple 3:1 basis. Bever (1) obtained a buff-colored barley smut from the F_3 population of a hybrid between *Ustilago nigra* and *U. hordei.* Sporidial fusions in culture indicated two sex compatibility factors, and failure to obtain infection with paired monosporidial lines and chlamydospores indicated a difference in factors governing sex and pathogenicity. A weakly pathogenic albino strain of *Ustilago nuda,* believed to have arisen by mutation, was reported by Mastenbroek (71), and Campagna (8) earlier reported a " white loose smut " of wheat, the spores of which would not germinate.

Hybridization between two races of *Ustilago hordei* during passage through the host was demonstrated by Tapke (106) who inoculated a susceptible variety with a mixture of races 3 and 5. A race different from either parent was obtained, and its pathogenic properties indicated that it had arisen through hybridization between the two races in the mixture. Hybridization not only between races of *U. hordei* but also between this species and *U. nigra* may occur. Bever (3) obtained new races from inter- and intraspecific crosses involving these species, but no simple Mendelian inheritance ratios could be demonstrated. For example, in the F_1 generation both loose and covered types of smut occurred with a complete range of intergrading types. In backcrosses with *U. hordei* the covered smut head type predominated, while similar crosses with *U. nigra* produced a wide range in type of smutted heads. Although the echinulate character of *U. nigra* chlamydospores was

dominant over smoothness in *U. hordei* spores, there was no precise ratio of echinulate and smooth spores in the F_2 generation. Independent segregation and recombination of factors for type of smutted head and chlamydospore markings was indicated. Heads of the loose smut type usually had echinulate spores, while those of the covered smut type had either echinulate or smooth spores with about equal frequency. New pathogenic types, combining the attributes of both parent species, were obtained. The intermediate nature of *Ustilago medians* and *U. nigra* suggests their possible origin through hybridization between *U. hordei* and *U. nuda* (103, 104).

Hybridization between *Ustilago avenae* and *U. perennans,* for which no common host is known, was reported by Holton and Fischer (49). Infection was obtained on wild oats (*Avena fatua* L.), host of the *U. avenae* parent but not on tall oatgrass (*Arrhenatherum elatius* (L.) Mert. and Kock), host of *U. perennans.* Segregates with the *U. avenae* pathogenicity were obtained by inoculating oats, but no *U. perennans* segregates were recovered from inoculation of tall oatgrass. Subsequently Fischer and Holton (23) demonstrated the heritability of sorus characters in these hybrids. Naked and powdery characters were dominant over covered and indurate, respectively, and inheritance of these characters was on an independent basis.

Inheritance of spore markings was on an independent and irregular basis in crosses between *Ustilago hordei* from *Elymus canadensis* L. and *U. bullata* (21). According to Fischer (21), color, echinulation and size of spores were the principal differences noted. Fischer (22) also was able to hybridize *U. striaeformis* and *U. bullata.* The F_1 sori were of the striate type characteristic of the former species, and there was a tendency for sporulation to occur in the glumes and flag leaf instead of the lower leaves. Segregation in the F_2 generation was irregular. The F_1 spores were minutely echinulate in contrast to the prominent spines of *U. striaeformis* and the roughly verrucose texture of *U. bullata.* Both parental types were recovered in the F_2 generation, each being associated with its original sorus type.

The genetic basis for variability in the wheat bunt fungi (*Tilletia caries* and *T. foetida*) is well established. Holton (42) concluded that pathogenicity in both species is controlled by multiple factors and that factors for pathogenicity and spore morphology are inherited independently. The smooth spore character of *T. foetida*

was dominant in eight hybrids, while only partial dominance was expressed by the reticulate character of *T. caries* in 24 hybrids (44). Sorus type was controlled by genetic factors, but the manner of inheritance was not indicated. Holton and Lowther (51) observed that differences in the number of primary sporidia produced by certain races of *T. caries* and *T. foetida* were controlled in an irregular pattern in crosses between races within each species. Dominance for small number and single factor differences were indicated in some crosses but not in others. Segregation and recombination of factors in the F_2 generation produced spores with large, intermediate and small numbers of sporidia, but no ratio could be established. The action of complementary factors was indicated by the fact that some segregates produced significantly larger numbers of sporidia than the parent race. A recent report by Holton (46) presents further evidence for segregation and recombination of factors for reticulate and smooth spores as well as some indication of heritability of factors for rate of germination in chlamydospores. All evidence of heterothallism and hybridization in the bunt species on wheat is questioned by Halbsguth (29) who states that erroneous conclusions have been drawn on the basis of certain false assumptions. Halbsguth presented no data to support his position.

The significance of induced hybridization in the bunt species and races in relation to their natural occurrence is indicated by the problem of nomenclature. Gassner (24) described an intermediate type occurring in a field collection containing both species and designated it as *Tilletia tritici* f. *intermedia.* Hirschhorn (37) described several hybrid forms or races with morphological characters distinct from *T. caries* and *T. foetida* among field collections studied by her. Savulescu and Hulea (94), Hulea (54) and Grasso (26) reported intermediate types in field collection and recognized four species of wheat bunt. All of the intermediate types observed in field collections bear a marked resemblance to the types occurring in artificially produced hybrids (44).

SUMMARY AND CONCLUSIONS

Physiologic specialization is a major factor in the perpetuation of smut disease problems. Genetic relationships, particularly with respect to interbreeding among variable types, contribute to the dynamic nature of the smut fungi. Their adaptability seems un-

limited. This situation, therefore, portends a continuous struggle to contain the smut diseases within the limits necessary for economic production of basic agricultural crops. Fundamental to this objective is an expanding concept of the natural attributes of the smut fungi. This can be gained only through the medium of a well-balanced research program, considering both the fundamental and practical aspects of the problem. Obviously specialization and genetic relationships are important phases of the research on smuts, and the information of these aspects of the subject has increased appreciably in the last decade. An attempt has been made here to summarize and relate the contributions of the last 12 years and to focus attention on the need for additional work.

Specialization is common-place in virtually all smuts. Wide differences in degree of specialization exist among various species, depending to some extent on methods of race identification. Pathogenicity is the primary basis for race differentiation in most of the smuts, and its significance is self-evident. Changing race populations frequently determine crop variety populations. Conversely crop varieties may determine smut race population by the selective influence on hybrid inoculum. Standardization and coordination of race studies with the breeding of smut-resistant varieties has increased the effectiveness of smut control by this method. This is best exemplified in the work with smuts of wheat, oats and barley, while work along this line with grass smuts is just beginning.

Characteristics other than pathogenicity by which physiologic races may differ include rate and kind of spore germination, minor differences in spore morphology, effect on host morphology, tendency toward lysis and growth type in culture.

Variability in the smut fungi is determined primarily by their genetic constitution. A high degree of gene complexity exists in most species. Sex compatibility factors range from simple to complex ratios. In most smuts heritability of factors for pathogenicity, spore morphology, germination type, tendency toward lysis, mutability and culture characters is on a multiple factor basis. Tendency toward lysis may be associated with sex and solopathogenicity. Meiosis may be completed in the first two divisions of the diploid nucleus or delayed to the third or fourth division.

Mutation frequently gives rise to new races. In corn smut mutability and sporidial fusion in culture may be influenced by the

nutrient content of the medium. Biochemical mutants of *Ustilago zeae* have been produced, and their potential value as a tool in genetic studies has been emphasized. Several albino or white mutant races have been reported.

New pathogenic races may be produced experimentally in some smuts by hybridization between species and races. In the oat smuts the pathogenicity of any race may be transferred to another by certain procedures of hybridization and selection. Species without a common host may be induced to hybridize. Heterosis has been indicated in certain hybrids of sorghum smuts and wheat bunt. Evidence that natural hybridization occurs is indicated by certain field collections of chlamydospores that resemble those of artificially induced hybrids (44).

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FOSSIL CHAROPHYTES

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INTRODUCTION

Fossil charophytes are found principally, but not exclusively, in calcareous shales and limestones that have been deposited in fresh or brackish water. The limited distribution of these sediments, combined with the great difficulty of arranging the fossil forms systematically, has led to neglect of the group by most paleontologists and paleobotanists. The principal systematic papers that have been published in the past 20 years are those by Peck (1934*a*) and Croft (1952) on the Paleozoic Charophyta; the monograph by Harris (1939) on the Purbeck Clavatoraceae; and the extensive consideration of the post-Paleozoic charophytes of Hungary by Rasky (1945).

There have been comparatively few specialists on the Charophyta, and most of them have dealt largely with the living forms. Mr. James Groves of England was one of the few workers of the twentieth century who could claim extensive knowledge of both living and fossil charophytes. Fortunately, Groves recorded his observations in several papers, two of which are of exceptional importance for the student of fossil forms. In 1924 he wrote a summary on the "Geological History of the Charophyta", and in 1933 he published a bibliography on fossil charophytes and listed all known species in Fossilium Catalogus, Plantae.

Because of the excellent quality, completeness and ready accessibility of these two contributions by Groves, this paper attempts primarily to summarize the work done since their publication.

Bibliographic references are adequately given by Groves (1933), Peck (1934*a*), Rasky (1945), Peck and Reker (1948*a*) and Croft (1952). The bibliography accompanying this paper lists only those publications mentioned in the text.

The writer is grateful to Mr. W. N. Croft of the Geological Department of the British Museum (Natural History) for furnishing galley proofs of his paper on "A new *Trochiliscus* (Charophyta) from the Downtonian of Podolia". This British Museum Bulletin

was published early in 1952. Mr. Croft also read an early draft of this paper and made many excellent and helpful suggestions.

PRESERVATION

The Charophyta are generally represented as fossils by the calcified portions of the oogonia (gyrogonites). On some forms (*Aclistochara* and *Karpinskya*) coronula cells or evidence of their former presence are preserved, and in *Clavator* the utricle (adnate cells enclosing the oogonium) is present on many fossils. Most of the plant secretes calcite, but generally this material loses its organic structure and disintegrates into a fine-grained mud when the organism dies. The secretion within the enveloping cells, and on some forms within the coronula cells, are the portions that most consistently maintain their form. In special conditions of preservation portions of the vegetative part of the plant are preserved. Notable examples are in the Purbeck of England, where vegetative parts have been silicified and are preserved in great detail, and in the Jurassic Morrison formation of the Rocky Mountain region, where some of the limestones are composed almost entirely of charophyte vegetative parts.

Charophyte fossils most commonly occur in non-marine sediments. Occasionally gyrogonites are found in association with marine fossils, but such occurrences are probably the result of transportation of the charophytes as clastic sediments. The Paleozoic Trochiliscaceae and Sycidiaceae occur, in some places, in marine sediments in association with marine fossils, but Croft (1952) has considered all available evidence and concluded that their habitat was non-marine.

Charophyte fossils may be composed of calcite, or the original calcite may have been replaced. If the charophytes have been silicified, as in the British Purbeck, they can be readily freed from a limestone matrix by acid. Charophytes preserved as calcite are extremely difficult to free from a limestone matrix. Under such circumstances the most successful method of collecting the fossils is to gather shale or clay partings associated with the limestone. The shale or clay is then soaked in water and boiled or washed, occasionally decanting and flushing with clean water. When a clean residue is obtained it is dried and the charophytes picked out with a damp brush or needle under a binocular microscope.

CLASSIFICATION

Charophyta, living and fossil, are here grouped into four families —Characeae, Clavatoraceae, Trochiliscaceae, Sycidiaceae. Of the four other family divisions that have been proposed, the Paleocharaceae (Pia, 1927) and the Kosmogyraceae (Stache, 1889) are grouped with the Characeae, and the Atopocharaceae (Peck, 1938) are referred to the Clavatoraceae. The Lagynophoraceae Stache (1889) were considered a subfamily of the Characeae by Pia (1927) and were again raised to family rank by Rasky in 1945. These forms are incompletely known and may belong to the Clavatoraceae (Harris, 1939, p. 65).

TROCHILISCACEAE AND SYCIDIACEAE

The Trochiliscaceae and the Sycidiaceae, Paleozoic charophytes and known collectively as the trochilisks (German-Trochilisken, written trochiliscids by Peck), have been the source of considerable vexation among systematists. They were first recorded as "polyps", and since have been variously referred to as fish eggs, phyllopod eggs, echinoids, foraminifera and various types of algae (Peck, 1934*a*, pp. 84–85). As late as 1933, Groves failed to recognize any relationship between the trochilisks and living or fossil charophytes.

The trochilisks have been the subject of three detailed papers within the past 50 years, each paper attempting to prove that they were Paleozoic Charophyta. Each writer in turn has recognized the validity of the evidence and of arguments set forth by the preceding and has gone on to advance additional arguments until now the evidence supporting the charophyte affinities of the trochilisks seems irrefutable.

The first of these papers, and probably the most notable because of its careful work and pioneering character, was by Karpinsky in 1906. In an elaborate and well illustrated monograph with both Russian and German text, Karpinsky described the trochilisks of the Middle and Upper Devonian of Europe. He gave an historical review of previous work, careful consideration to the morphology of the gyrogonites and their wall structures, and proposed two generic divisions, *Trochiliscus* and *Sycidium*. Each genus was the type of a separate family written with the zoological family name suffix—Trochiliscidae and Sycididae.

Additional evidence for the charophyte affinities of the trochilisks was given in a paper on the North American forms by Peck (1934*a*). The chief contributions of this paper were the descriptions and illustrations of calcified coronula cells preserved on some of the Upper Devonian and Lower Mississippian forms, and the establishment of an English terminology for the description of these relatively unknown fossils. A later paper (Peck, 1936) described another occurrence of the Trochiliscaceae from an unnamed shale of probable lower Middle Devonian age in Ralls County, Missouri. In this paper it was noted that apparent evolutionary trends within the Trochiliscaceae consisted of an increase in size, a reduction in the number of spirals (enveloping cells), and establishment of the ability to secrete calcite in the coronula cells.

The latest contribution on the systematic position of the trochilisks is a remarkably detailed and careful description of a new species of *Trochiliscus* from the Downtonian (Lower Devonian) of Podolia (eastern Europe in Russian territory) by Croft (1952). The details of the structure of the lime-shell and the interiors of the gyrogonites are remarkably well preserved, and Croft was able to show that the layering of the calcareous gyrogonites and the details of the oospore membrane were very similar to those of living charophytes.

The Trochiliscaceae are represented exclusively by dextrally spiralled gyrogonites composed of from seven to 18 units. They are known only from the Devonian of the European and North American continents, and from a single locality in the basal Lower Mississippian of North America. The oldest recorded occurrence is that recently described by Croft (1952) from the Lower Devonian (Downtonian) of Podolia. Other European occurrences are chiefly in the Middle and Upper Devonian of Germany, Russia and Esthonia. In North America the Trochiliscaceae are rather widely distributed in the Lower (Onondaga) and Middle or Upper Devonian of Ohio, Michigan, Iowa and Missouri. They have also been recorded but not described from the Devonian (Onondaga) of central western Canada (Fritz, 1939), and bodies that possibly represent trochilisks have recently been described from the Devonian of Texas (Ellison and Wynn, 1950).

The Sycidiaceae are small spherical fossils, averaging about 1.0 mm in diameter and having a reticulate surface, the reticulation

caused by the crossing of from 16 to 20 longitudinal ridges by horizontal ridges. The Sycidiaceae bear little resemblance to charophytes and were referred to them originally because of their association with the Trochiliscaceae. Detailed evidence on the construction of the outer wall of the Russian forms (Karpinsky, 1906), and identification of the oospore membrane in specimens from Europe by Karpinsky and from the United States by Peck (1934*a*), have more firmly linked these small fossils with the charophytes.

The Sycidiaceae are found in association with the Trochiliscaeae in many places, but representatives of each family occur without the other. Trochiliscaceae are well represented in North America, both geographically and geologically, but the Sycidiaceae are known only from the Lower Mississippian Bushberg formation of central Missouri and from the Waterways formation on the Athabasca River, Canada (unpub.). Both the Sycidiaceae and the Trochiliscaceae occur commonly in the Devonian of central Europe, but they are not always found together. Hacquaert (1932*a*, 1933) reported *Sycidium* from the Belgian Congo, but his identifications were made from thin sections, and Pia (1937, p. 777) believed the specimens to be ooliths. Lu (1948) has recorded Sycidiaceae without Trochiliscaceae in China.

Hacquaert (1932*c*) noted the presence of a small problematical fossil in the Silurian of Turkestan under the name *Pseudosycidium* Karpinsky. In so far as the writer has been able to learn, this genus has never been formally described or named, and the relationship of the fossils with charophytes has not been confirmed.

Karpinsky subdivided the trochilisks into two clearly differentiated genera, *Trochiliscus* and *Sycidium*, and set up separate families, the Trochiliscidae and the Sycididae. On the material available to him he established two species of *Trochiliscus* and two species and one variety of *Sycidium*. Karpinsky also discussd characters that might be used in specific differentiation in both genera.

For *Trochiliscus*, Karpinsky (1906, p. 122) listed as characters for specific differentiation: the shape of the gyrogonites; the size and number of spiral ribs; and the ornamentation, or the comparative width of the ridges and furrows. Karpinsky pointed out that, for his two species, the number of spiral ribs appeared to be normally nine and 18, respectively, but that the nine-spiralled form

might vary from eight to ten, and that variants of the 18-spiralled form might possess 16 or 20 spirals.

In describing the North American species, Peck (1934*a*) used the criteria proposed by Karpinsky and, in addition, the two characters (p. 101) of "constant variations in the part of a complete turn about the oogonium (gyrogonite) made by the spiral cells", and the "consistent presence or absence of coronula cells". Peck considered the number of spirals, representing the number of enveloping cells on the living plant, of great importance and did not allow for variations of this character within a species as was done by Karpinsky.

Croft (1952) took exception to the importance placed by Peck on the number of spirals. He cited numerous examples of individual variations in living charophytes and other plants, living and fossil, and found similar variation in the number of vertical rows of plates in the coronas of Paleozoic echinoids. Croft regroups the North American forms, reducing the number of species from 15 to five. In his new grouping, Croft gives more emphasis to size, convolution and association, and less to the number of spirals.

Until recently all dextrally spiralled gyrogonites have been referred to the genus *Trochiliscus*. Croft (1952) stated that the presence or absence of recognizable coronula cells is of definite taxonomic value and proposed two subgenera founded mainly on this character. The sub-genus *Euthrochiliscus* contains the non-coronulate forms and the sub-genus *Karpinskya* the coronulate forms.

Modern Charophyta live only in fresh or slightly brackish water, and most post-Paleozoic fossil charophytes occur in non-marine sediments. One of the objections to the acceptance of the trochilisks as charophytes has been their fairly common occurrence in association with marine fossils. Croft (1952) has considered this question carefully and has concluded that the trochilisks lived in a non-marine environment. A summary of his evidence is as follows:

a) The trochilisks of Europe and China occur in sediments that can be interpreted as of non-marine origin. Generally the only associated fossils are ostracodes and fishes.

b) The trochilisks of North America occur chiefly in the basal deposits of advancing seas. It is quite possible that the charophytes lived in brackish water lagoons or in fresh water streams and lakes

and were transported into a marine environment to be buried in association with marine fossils.

c) The resistant membrane around the oospore probably contained food reserves in the form of starch. This would indicate adaptation to periods of desiccation, a characteristic of land plants.

In North America the trochilisks occur chiefly in formations of unquestioned marine origin and in most cases in association with abundant marine fossils. In the Snyder Creek, Cerro Gordo and Bell shales the trochilisks are scattered and comparatively rare. It is well known among micropaleontologists that occasional charophyte gyrogonites are commonly found in samples from present day marine beaches and shallow water deposits. The trochilisks occur in these Paleozoic shales in about the same proportion and may well represent gyrogonites washed into a marine environment.

The trochilisks are found at a single locality in the Bushberg and are present there in great abundance. No other fossils are associated. The Bushberg is the basal deposit of the advancing Mississippian sea and at this locality is only about six inches thick. The abundance of trochilisks could easily be the result of a concentration by washing into the beach, or it could represent a lagoon or lake at the edge of the advancing sea.

The trochilisks are very abundant in the shale at the base of the Mineola, and the only associated fossils are smooth characterless ostracodes of uncertain affinities that give no aid in determining habitat. It is probable that these shales are lacustrine in origin.

The trochilisks in the Columbus and Jeffersonville limestones present a more difficult problem. These occurrences may be compared to the abundance of charophyte gyrogonites in the Eocene Ocala limestone of Florida, a formation of unquestioned marine origin (Peck and Reker, 1948*a*).

The North American occurrences offer no difficulty to the acceptance of Croft's conclusion that the trochilisks were fresh-water plants.

CLAVATORACEAE

In 1916 Reid and Groves published a preliminary paper on some peculiar charophytes from the British Purbeck (Jurassic) and proposed for them a new generic name, *Clavator*. It was the intention

of these two workers to continue their studies of the Purbeck charophytes, but they never completed the work. It was left to Harris (1939) to fully describe these forms in an excellent and detailed monograph.

Most fossil charophyte remains are preserved as gyrogonites[1] alone or with disassociated vegetative parts in limestone and calcareous shale. With such preservation it is impossible to determine the characters of an entire plant, and usually impossible to determine which vegetative parts belong with particular gyrogonites. Many of the charophytes in the Purbeck occur as silicified fossils in limestone and are readily dissolved out of the limestone matrix by application of HCl. By preparing the material in this manner, Harris was able to identify and associate reproductive and vegetative organs and to work out details and relationships among the Clavatoraceae to a much greater extent than has been possible with other occurrences of charophyte fossils.

The family is defined by Harris (p. 14) as "charophytes with a corticated axis: branches arising alternately with leaves and without disturbing the cortical cell rows. Oogonia having their outer walls calcified, as well as the inner walls of the spiral cells".

The Clavatoraceae are highly organized charophytes. The genus *Clavator* is compared with the more robust species of *Chara* (Harris, 1939, p. 16), and the following differences are listed:

"1. The branches (of *Clavator*) alternate with the leaves instead of being axillary.

2. The leaves of successive whorls are superimposed instead of alternating.

3. The cortex consists of continuous series of cells which are not interrupted in the middle of an internode, as in recent corticated Charales. Evidently it is formed in a different way.

[1] There is considerable variation in the use of the terms "oogonium", "gyrogonite", and "fruit", in papers on fossil charophytes. Most workers have used the terms "oogonium" and "fruit" for the spiralled calcareous body, commonly found fossil. Harris (1939, p. 12) found that both the outer walls and inner walls on the enveloping cells of the Clavatoraceae were calcified, and he suggested that the term "gyrogonite" be used when only the inner walls are calcified, which is the usual case. Harris continued to use the term "oogonium" when both the outer and inner walls were preserved (p. 15, 33). Croft (1952) stated that the term "oogonium" should be reserved for the "egg cell together with its sheath of sterile enveloping cells" and that the term "gyrogonite" should "be used to include all fossil charophyte fruits, irrespective of the number and direction of enveloping cells".

4. The cortex consists of six 'primary' and six 'secondary' series of cells; but the six 'secondary' bear spine cells in exactly the same way as the 'primary'. In recent Charales with secondary cortical series (diplostichous) these cells are distinguished by being without spines.

5. The swelling of the six 'primary' cortical series at the node is peculiar.

6. The outer wall of the oogonium is calcified, as well as the inner.

7. The outer wall of the oogonium often shows conspicuous blunt knobs.

8. The oogonium is invested in a utricle".

Harris describes three species of the genus *Clavator* in great detail.

The genus *Perimneste*, with one species, was defined by Harris (p. 54) as having each oogonium surrounded at maturity with leaf segments bearing antheridia, and the walls of the antheridia calcified. The oogonia are not enclosed in utricles.

The vegetative organs are thinly calcified and not so abundantly preserved as those of *Clavator*. The leaves are not corticated and bear a few simple spinelike leaflets in small whorls. The node bears 18 leaves in three whorls of six. One whorl of upward pointing long leaves is on the same radius as the cortical cells, and two whorls of short leaves are on alternate radii, one pointing upward and one downward.

A new form-genus, *Charaxis*, is proposed by Harris (1939, p. 67) for vegetative organs agreeing so far as known with the genus *Chara*.

The Clavatoraceae are widely distributed in Jurassic and Lower Cretaceous non-marine deposits. The genus *Clavator* has been recorded from Germany (Bruckner and Pia, 1935), from the Purbeck of the Swiss Alps (Carozzi, 1948), from the middle chalk of Hungary (Rasky, 1945), and is widely distributed in the Lower Cretaceous of North America (Peck, 1941, Peck and Reker, 1948*b*). Antheridia of the genus *Perimneste* are present in the Lower Cretaceous of Idaho (Peck, 1941), and it is probable that the gyrogonites are also present in North America but have been misidentified. A third genus, *Atopochara* Peck (1938), was misinterpreted in the original description and was referred to the Clavatoraceae a few years later (Peck, 1941). *Atopochara* is

common in the non-marine Lower Cretaceous of North America and has been recorded from strata of similar age in Hungary by Rasky (1945) and in Syria (Van Bellen 1948).

In 1889 Stache described the genus *Lagynophora* from the lower Tertiary of the Italian Alps. The description and illustrations are not sufficiently detailed to allow close comparison with the Clavatoraceae. Pia (1927) considered *Lagynophora* of subfamily rank in the Characeae; Stache (1889) and Rasky (1945) considered the genus as the type of a new family; and Harris (1939, p. 65) stated that it is quite possible that *Lagynophora* is closely related to *Perimneste*. Both the outer and inner walls of the oogonia of *Lagynophora* are calcified, as in the Clavatoraceae. If Harris is correct the range of the Clavatoraceae is from Upper Jurassic to Paleocene.

Maslov (1947) has demonstrated that *Chara meriana* from the Russian Tertiary also has the inner and outer walls of the oogonium calcified, as in the Clavatoraceae. It is quite possible that future detailed investigations will greatly extend the geographical and geological range of the family Clavatoraceae.

CHARACEAE

The Characeae are the modern living representatives of the Charophyta. The family is divided into two subfamilies: the Chareae with five coronula cells arranged in one tier on the oogonium, and the Nitelleae with ten coronula cells arranged in two tiers. The enveloping cells do not calcify on most living species of the Nitelleae, and few fossil forms have been referred to this subfamily. The Chareae are long ranged and abundant, starting in the Pennsylvanian period of the Paleozoic era and becoming more important as the present day is approached. For the most part, the fossil species are represented by the calcified inner walls of the oogonia (the gyrogonites), but in a few instances calcified portions of the vegetative organs occur.

The Paleozoic record of the Chareae does little more than prove their presence. Sinistrally spiralled gyrogonites occur sparsely in the Pennsylvanian sediments near Columbia, Missouri, and in the lower Permian near Manhattan, Kansas (Peck, 1934*b*). They are also present in the Pennsylvanian of Nova Scotia (Bell, 1922). In the Missouri and Kansas localities the gyrogonites are com-

paratively rare and are in association with marine fossils. It is quite probable that they have been carried into the marine environment as small clastic particles. The forms recorded from Nova Scotia are unique in that they possess six sinistrally spiralled units. Pia (1927) and Rasky (1945) have given this genus family rank as the Paleocharaceae.

The Triassic record is of little importance. One species has been described from the upper part of the Chugwater Group (Jurassic ?) of Wyoming (Peck, 1934*b*), one from the Upper Triassic or Rhaetic from the Belgian Congo (Groves, 1933), a few gyrogonites have been reported from the lower Keuper of Sweden (Brotzen, 1950), and reference is made to oogonia in the Lower Bunter sandstone of Prussia (Krause, 1938).

Occasional occurrences of charophyte gyrogonites have been recorded from the marine Jurassic of Europe and North America. In most of these instances the gyrogonites were probably carried as fine clastics and deposited in a marine environment.

In the Morrison (Jurassic) formation of the Rocky Mountain region gyrogonites and vegetative organs of charophytes occur in abundance. These forms were partially described in a short preliminary paper by Peck (1937). Peck described only the gyrogonites and referred them either to the genus *Chara*[2] or to a new genus, *Aclistochara*. All gyrogonites with the spirals coming together to form a closed summit with no opening were referred to *Chara*. Gyrogonites with open summits and definite indications of calcified cornula cells were placed in *Aclistochara*. A comprehensive study of large collections of gyrogonites and vegetative organs from the Morrison is currently being made by the writer,

[2] A difference of opinion has arisen among workers on fossil charophytes as to the use of the generic name *Chara*. Pia (1927) included all oogonia (gyrogonites) with five smooth chalk bands on the fruits, which could not be provisionally assigned to a natural genus, to the form-genus *Gyrogonites* Lamarck. Peck (1934*b*) followed the suggestion of Pia but in 1938 returned to the use of the name *Chara* for gyrogonites not referable to other genera and not definitely differentiated from the gyrogonites of living *Chara*. Harris (1939) argued for the use of the name *Gyrogonites*, pointing out that it is impossible for some gyrogonites described as species of *Chara* to be distinguished with certainty from genera of the Clavatoraceae. Croft (1952) supports the arguments of Harris, pointing out that it is impossible to be certain that these gyrogonites do represent *Chara*, and therefore it is more correct to refer them to a form-genus. Many students of charophytes continue to refer species of fossile gyrogonites that agree in all essential details with the gyrogonites of *Chara*, to that genus.

and it is probable that several of the Morrison species will be referred to genera in the Clavatoraceae.

Mittre (1952) has described some very small oospores found in thin sections of chert from the Jurassic of southern India. He referred the oospores to the Nitellae.

Both *Aclistochara* and *Chara* (*Gyrogonites*) are well represented in the Lower Cretaceous non-marine deposits but are overshadowed in both numbers and importance by representatives of the Clavatoraceae (Peck, 1941).

Charophytes from the Upper Cretaceous have not been extensively studied. A few species have been described from North and South America (Groves, 1932; Peck and Reker, 1947) and from Hungary (Rasky, 1945), but these have mostly been isolated occurrences. In the non-marine Upper Cretaceous of the Rocky Mountain area in North America and the Andean area in South America more intensive collecting and study should give good results from both stratigraphic and systematic viewpoints.

Rantzien (1951) has recently completed an informative survey of the occurrences and classification of the fossil Charophyta of Latin America. He stated that the range of known forms in Latin America is from Lower Cretaceous to Pleistocene.

The Chareae were quite important during the early Tertiary. The non-marine Tertiary formations of Europe contain these small fossils in abundance, and extensive and important contributions were made in the latter part of the nineteenth and early part of the twentieth centuries by workers in England, France, Switzerland, Hungary, Germany and Austria (see Groves, 1924, 1933). In recent years the only important European contributions have been by Klara Rasky (1941, 1945) who, in a well illustrated and detailed monograph (1945), describes five Cretaceous, 12 Paleocene, one Eocene, 14 Oligocene and three Miocene species.

In Asia the Chareae have been used in determining the age of part of the Deccan traps and have been extensively investigated in recent years (papers by Rama Rao, Narayana Rao, Sripado Rao and B. Sahni, 1936–43). These authors described and illustrated the Indian assemblages and compared them with known forms from Europe and America. A few Chareae have also been recorded from China by Lu (1944–45).

In the Americas isolated occurrences of Chareae have been reported from time to time (Groves, 1933), but the first attempt at

a fairly comprehensive consideration of Tertiary charophytes was made by Peck and Reker (1947, 1948*a*). In two short papers these writers described three species from the early Tertiary of the Andean region in Chile and five from the northern Rocky Mountain region and Florida of North America. Some species of *Aclistochara* from North America illustrate beautifully the preservation of coronula cells. Both papers contain illustrations of species with tubercles on the spiral cells, a character that led Stache to differentiate the genus *Kosmogyra*. Peck and Reker concluded, after studying large collections, that the tubercles may or may not be present on a species and that, if present, they may be represented by varying degrees of prominence. They therefore included *Kosmogyra* as a synonym of *Chara*.

Later Tertiary formations contain many charophyte remains but they have not been comprehensively studied or described.

CHAROPHYTES AS STRATIGRAPHIC FOSSILS

One of the principal objectives of much of the work on fossil charophytes has been an attempt to establish recognizable groups with limited ranges in geological time. Potentially they are excellent stratigraphic fossils. The gyrogonites occur in abundance in great thicknesses of non-marine strata and often are the only fossils available by which geologic age may be determined. Students of fossil charophytes have long sought to determine criteria by which the large numbers of gyrogonites could be classified, named and used for correlation purposes.

The results to date have not been encouraging. The gyrogonites are composed of the calcified inner walls of the enveloping cells of the oogonium. Some forms have the coronula cells preserved (*Karpinskya, Aclistochara*), and others are distinguished by possession of utricles (*Clavator, Atopochara*). These forms are rather easily differentiated and are widely distributed with fairly limited geologic ranges. But by far the greater majority of the gyrogonites are simply the calcified inner portions of the enveloping cells and can be differentiated and classified at best only on size, shape, degree of calcification, and angle and direction of ascent of the spirals (equatorial angle of Peck, 1934*a*). All of these characters are difficult to limit and use, especially when so little is known of the variation on living species.

Harris (1939, pp. 75–79) made a detailed study of a single

gathering of *Chara vulgaris*, a modern species. He concluded that the length and breadth of the gyrogonite varied ± 20% from a mean, that there was a good deal of variation in the shape, and the angle of ascent of the spirals varied within ± 2%.

Harris came to the conclusion that the range of variation of the gyrogonites within the family did not appear great enough to allow a very large number of specific groups to be distinguished, and that the gyrogonites are likely "to have only slight stratigraphic value".

The systematic arrangement of fossil charophytes has been further complicated by the description of a great many isolated species by different authors with no attempt to compare and contrast their material with previously published work.

In spite of the difficulties cited above, the charophytes are proving to have some stratigraphic value. Where they occur in considerable abundance, as in the Devonian, Jurassic, Cretaceous and lower Tertiary deposits of North America, it is found that assemblages, at least, are recognizable and can be placed stratigraphically. It is probable that gyrogonites will never be of great value in the determination of detailed stratigraphic units, but they are becoming useful in the determination of geologic periods, series and sometimes stages. Perhaps the way pointed in the recent papers by Maslov (1947) and Croft (1952) in the study of gyrogonites by thin sections will prove of value in further refinement in classification and closer and better determination of species. One of the things most needed at present is a detailed study of gyrogonite assemblages, both known and new, the inclusion of many specific names in synonymy, and more clear-cut and lucid definitions of the recognizable forms.

EVOLUTION OF THE CHAROPHYTA

The oldest definite charophyte so far recorded is *Trochiliscus* (*Eutrochiliscus*) *podolicus* Croft from the Lower Devonian of Podolia in eastern Europe. Even at that early stage many of the characters considered peculiar to the charophytes had already been established. The oospore was enclosed in spiral enveloping cells that secreted calcite along the inner margins as do living species of *Chara*; there was already present a thickened resistant membrane around the oospore that probably contained food reserves

and indicated adaptation to periods of dryness; and associated fossils indicated that they were inhabitants of fresh-water streams and lakes. The dextrally spiralled Trochiliscaceae and their near relatives and associates, the reticulate Sycidiaceae, persisted through the Devonian and made their last recorded appearance as silicified gyrogonites in basal deposits of Lower Mississippian age in central Missouri. During the Devonian the Trochiliscaceae increased in size, decreased in general the number of spiral enveloping cells, and acquired the ability to secrete calcite in the coronula cells.

There is no record of charophytes in rocks of Middle and Upper Mississippian age. The next record consists of gyrogonites with five sinistral spiral units in rocks of Middle Pennsylvanian age in central Missouri and gyrogonites described as possessing six sinistral units (*Paleochara* Bell) from the Coal Measures of Nova Scotia. Since Middle Pennsylvanian time of the Paleozoic era the five sinistral enveloping cells of the charophyte oogonium has been well established, and any deviation from the number five can be considered individual and aberrant.

Little is known of charophyte history during the Late Paleozoic and Early Mesozoic. But in the Upper Jurassic Purbeck Beds the vegetative plan of the living genus *Chara* was already well established (Harris, 1939, p. 70). Such vegetative parts are referred to the form-genus *Charaxis* Harris. Also in Purbeck time the family Clavatoraceae was well established. The Clavatoraceae were, according to Harris (1939, p. 74), "the most elaborately organized members of the whole Charophyte class". This family was well represented and widely distributed during the Upper Jurassic and Lower Cretaceous, and, if *Lagynophora* Stache or *Chara meriana* (Maslov, 1947) belong to this family, the range is extended into the Tertiary.

Unfortunately neither the Paleozoic trochilisks nor the Mesozoic Clavatoraceae give any aid in explaining the ancestry or relationships of the class.

Charophytes of the Upper Cretaceous are not well known and add little to our knowledge of the evolution of the group.

Gyrogonites of early Tertiary charophytes have been extensively described and illustrated. Many are simple and non-diagnostic. However, in the Tertiary there occur many large gyrogonites, most

of them with calcified coronula cells. Other gyrogonites are distinguished by an abundance of prominent nodes on the spirals (*Kosmogyra* Stache). The nodose, the coronulate and the very large gyrogonites do not continue into Late Tertiary. Miocene and Pliocene gyrogonites are very similar to those of living species.

ADDENDUM

An important paper on charophytes of the Kimmeridge (Jurassic) of northwest Germany was published by Mädler in August of 1952 and reached the writer too late to be included in the manuscript of this article.

Mädler described three new genera consisting of 21 new species, varieties and forms, and proposed a new classification for the charophytes. The new genera are: *Kosmogyrina,* gyrogonites with a closed summit and tubercles in intercellular furrows, type species *Chara andreanszkyi* Rasky; *Obtusochara,* small gyrogonites with truncated summit and without sunken furrows, spiral cells converging normally, type species not designated but becomes *O. prima* by monotypy; and *Sphaerochara,* gyrogonites with the summit structure of Chareae and more or less spherical form without decoration, type species *Chara hirmeri* Rasky. Mädler described one new species of *Clavator;* one new species of *Obtusochara;* four new species and one new form of *Tolypella;* and eight new species, two new varieties and three new forms of *Aclistochara.*

Mädler considered and rejected the proposal made by Pia in 1927 and advocated by Harris (1939) and Croft (1952) to use the form genus name *Gyrogonites* for all gyrogonites belonging to the Chareae or Nitelleae and not definitely referable to a living genus. Mädler prefers referring such gyrogonites to one of the genera already established or to one of his new genera. *Aclistochara* is discussed in detail, and the conclusion is reached that the generic characters proposed have sound biological basis and that the generic name should be retained. Several species of fossil charophytes named by various authors are discussed and referred to families and genera other than those originally designated.

By a series of drawings and text explanations, Mädler traces the formation of the charophyte oogonium and the development of the limeshell.

Mädler's new classification of the charophytes is as follows:

Class Charophyta

Order Sycidiales, new order
- Family Sycidiaceae (Karpinsky, 1906) Peck, 1934
  - Genus *Sycidium* Sandberger, 1849

Order Trochiliscales, new order
- Family Trochiliscaceae (Karpinsky, 1906) Peck, 1934
  - Genus *Trochiliscus* Karpinsky, 1906

Order Charales, new order
- Family Palaeocharaceae Bell, 1922
  - Genus *Paleochara* Bell, 1922
- Family Clavatoraceae Reid & Groves, 1916
  - Genus *Clavator* Reid & Groves, 1916
  - Genus *Atopochara* Peck, 1937
  - Genus *Perimneste* Harris, 1939
- Family Lagynophoraceae Stache, 1880
  - Genus *Lagynophora* Stache, 1880
- Family Characeae L. Cl. Richard, 1815
  - Subfamily Aclistochareae, new subfam.
    - Genus *Aclistochara* Peck, 1937
  - Subfamily Kosmogyreae Stache, 1889
    - Genus *Kosmogyra* Stache, 1889
    - Genus *Kosmogyrina*, new genus
  - Subfamily Nitelleae v. Leonhardi, 1863
    - Genus *Nitella* (Agardh, 1824) Braun, 1867, recent
    - Genus *Tolypella* (Braun, 1849) v. Leonhardi, 1863, fossil & recent
  - Subfamily Chareae v. Leonhardi, 1863
    - Genus *Obtusochara*, new genus
    - Genus *Sphaerochara*, new genus
    - Genus ? "*Charina*" Filarsky & Allen, recent
    - Genus *Nitellopsis* Hy, 1889, recent
    - Genus *Lamprothamnus* (Braun, 1876) Nordstedt, 1882, recent
    - Genus *Lychnothamnus* (Ruprecht, 1846) v. Leonhardi, 1863, recent
    - Genus *Chara* Vaillant, 1719, fossil and recent

Uncertain genera known only from vegetative remains
- *Palaeonitella* Kidston & Lang, 1921
- *Charaxis* Harris, 1939

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